

NICHE OVERLAP IN FEEDING ASSEMBLAGES OF NEW GUINEA BIRDS

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A SINGULAR opportunity for assessing the degree of niche overlap among elements of tropical avifaunas exists in the phenomenon of feeding trees. These contain fruit, flowers or some other food source that attracts numbers of animals, among which birds usually predominate. Since only a single commodity is available in most feeding trees, it is possible to compare the harvest by different species through some appropriate measure of tree usage. Consumption of a common resource by a number of species implies niche overlap and suggests that a state of competition at least potentially exists among the species.

The striking concentrations of birds that are frequently attracted to feeding trees in New Guinea have been remarked upon previously by observers working at widely scattered localities (Mayr and Rand, 1937; Rand, 1942*a* and *b*; Ripley, 1964). In their recent Handbook of New Guinea Birds, Rand and Gilliard (1967) comment on the significance of this phenomenon and point out the need for a systematic study.

The present paper gives an account of observations made at 20 feeding trees in the Eastern Highlands District of the Territory of New Guinea. Repeated censuses of the bird assemblages in each tree led to a time-dependent measure of feeding for each species present. The results allow estimates of the degree of niche overlap among the species taking certain classes of food (e.g., flowers, small fleshy fruits) and indicate the diversity of food sources exploited by particular species or groups of species.

METHOD

On finding an active feeding tree the observer sought the most advantageous viewing station, i.e., the point on the ground from which optimal lighting and visibility of the crown was obtained. In exceptional cases the entire face of a tree could be observed, but far more commonly intervening foliage reduced the exposure to a part of the crown or even a few branches. Consequently a large fraction of the birds using most trees was not seen.

Each tree studied was observed for one to several $\frac{1}{2}$ or 1 hour periods, each of which was comprised of a succession of two-minute censuses. The exposed portion of the feeding tree was systematically scanned with a pair of 8 \times 30 binoculars for approximately 1 minute and 45 seconds. During this time the observer accrued a mental tally of all the species and individuals seen. The remaining 15 seconds of these censuses were used to record the data. The two-minute census was selected when it was found that this was about the maximum time over which the observer could keep track of a cumulative mental tally of species and individuals in an active tree. It was a policy to maximize

the number of individuals rather than distribute the observation time evenly over all parts of the tree. No particular effort was made to find different birds with each new census, and thus the same individuals were often reeorded for a number of successive censuses.

A unit of tree-usage was derived from the census data on the assumption that a single sighting represented an average stay of two minutes in the tree. The justification of this assumption lies in the fact that the canopy area under observation was generally several times larger than that covered in one binocular field. Thus it was possible, on the one hand, for birds to come and go from the visible portion of the tree and escape detection, and on the other, for birds to remain visible for nearly 4 minutes and yet be reeorded in only one census. Since each observation represents a bird-usage of 2 minutes, the identification of one bird in each of the 30 censuses in a one-hour observation period would add up to a total of one bird-hour of tree usage. The number of bird-hours recorded in an observation period of any length is thus the aggregate of individual sightings divided by the number of two-minute censuses.

Once it had been ascertained several times that a species was actually taking food, all further individuals were tallied on the premise that they were in the tree for the purpose of feeding. The unexpected scarcity of transient species in feeding trees made it evident that virtually all the birds recorded in them had entered specifically to feed. In general the majority of individuals in a tree at any time were actively feeding, though social interactions or periods of rest or preening resulted in frequent brief interruptions.

The identification of more than 90 per cent of the bird species included in this report was confirmed by specimens collected in the localities of the trees but not from the trees themselves. Nomenclature follows that of Rand and Gilliard (1967). The feeding trees unfortunately cannot be identified since our collection of preserved plant material was lost. Thus brief descriptions from our field notes of the trees and their flowers or fruits must suffice.

All of the observations were made during the period of June to August, 1964, in the Eastern Highlands District of the Territory of Papua and New Guinea. A synopsis of the localities mentioned in the text follows. Karimui Patrol Post lies about 70 miles southwest of Goroka at 3,650 feet in an extensive mountain basin. Udo, Mao, Sordida, and Palea are native hamlets in the vicinity of Karimui. A flowering tree on the north bank of the Sena River was about 14 miles northeast of Karimui at an elevation of approximately 4,500 feet. A fruit tree near the village of Mengino I was at about 4,800 feet on the west slopes of Mt. Michael in the area administered from Lufa Patrol Post. Two localities were villages in the Fore language are administered from the Okapa Patrol Post, which is 36 miles southeast of Goroka: Mirassa at 5,800 feet and Okassa at about 3,500 feet.

RESULTS

Bird-usage data were recorded from nine flowering trees or lianas of four species, ten fruiting trees of at least six species, and one tree whose bark attracted large numbers of parrots. We will consider results from each of these general classes of feeding trees in order.

FEEDING ASSEMBLAGES IN FLOWERING TREES

White-flowered trees.—We were fortunate in locating five individuals of one species of flowering tree within a radius of 1½ miles of Karimui Patrol Post. These trees carried great numbers of dense umbel-like flower heads.

The individual blossoms were 3–4 mm across with conspicuous white petals and somewhat swollen glandular receptacles. All but one of the five trees stood at the edge of wide trails through original forest, the exception (Udo-2) being located in the forest some 200 yards to the side of a trail. Estimates of their heights fell between 100 and 120 feet, of which their leafy crowns comprised the upper 30–50 feet.

The bird usage of these trees was recorded in 2 to 5 one-hour observation periods. The results of repeated observations at a single tree showed little variation in the rank order of the 6 most frequent species (Table 1A). Bird-hour totals varied somewhat more and were particularly influenced by the large groups of lorikeets whose movements in and out of the tree were erratic. In general, the variation in results from different trees of the same species was greater than that among different readings from the same tree.

Averaged records from the five white-flowered trees are given in Table 1B. The preponderance of honeyeaters is immediately apparent. Members of this family alone accounted for 67–88 per cent of the species seen in these trees but comprised only 53 per cent of the observations. The small lorikeet, *Charmosyna placentis* was by far the most numerous species and accounted for 37 per cent of all observations. The list of species showed little variation from one tree to another, most of the exceptions being transients or occasional visitors. Of the 11 species that were regular users of these trees, all 11 occurred at two trees, 10 at one tree, and 9 at the remaining two trees.

While these trees were under observation, it became apparent that two of them were giving anomalous results with respect to the frequencies of some species. The third Udo tree attracted extraordinary numbers of *Oedistoma pygmaeum* and the *Myzomela* honeyeaters, while *Oreornis obscurus* was comparatively scarce. In contrast, at the Sordida tree the frequency of *Myzomela nigrita* was a factor of 10 less than in the third Udo tree and that of *Oreornis obscurus* was 30 times greater while *Myzomela cruentata* was altogether absent.

We suspected that these anomalous frequencies may have resulted from the facts that only the topmost branches of the third Udo tree were visible and that only the lower portion of the crown of the Sordida tree could be observed. This possibility was tested with the three white-flowered trees whose full crowns were visible. All subsequent observations on these trees noted whether the birds had been seen above or below imaginary horizontal bisectors of the crowns. A total of 965 sightings of 10 species were distributed, 51 per cent in the upper and 49 per cent in the lower halves of the crowns (Table 2). All but *Charmosyna placentis*, *Toxorhamphus iliolophus*, and *Xanthotis polygramma* were more or less unevenly distributed. The species that were disproportionately abundant in the third Udo tree, *Oedistoma pygmaeum* and the three *Myzomela* honeyeaters, were found to keep largely

TABLE 2

VERTICAL DISTRIBUTION OF SOME BIRD SPECIES IN THREE WHITE-FLOWERED TREES
IN THE KARIMUT REGION. PROBABILITIES FROM TWO-TAILED STANDARD
NORMAL VARIABLE TEST.

Species	No. of Observations	Per cent in Upper Half	Per cent in Lower Half	P
Parrots				
<i>Chamosyna placentis</i>	214	48	52	0.32
Honeyeaters				
<i>Oedistoma pygmaeum</i>	176	66	34	0.001
<i>Myzomela eques</i>	9	67	33	0.33
<i>Myzomela cruentata</i>	2	100	0	—
<i>Myzomela nigrita</i>	77	94	6	0.001
<i>Toxorhamphus iliolophus</i>	25	52	48	0.92
<i>Oreornis obscurus</i>	14	0	100	0.001
<i>Xanthotis chrysotis</i>	101	31	69	0.001
<i>Xanthotis polygramma</i>	79	46	54	0.35
<i>Meliphaga</i> spp. (six species)	256	36	64	0.001
Total	965	51	49	

to the upper branches. On the other hand, *Oreornis obscurus* appeared exclusively in the lower branches of the test trees, thus accounting for its extreme scarcity in the third Udo tree and relative abundance in the Sordida tree.

These data suggest that much of the observed tree-to-tree variation was due to fortuitous differences in the visibility of the canopy. When these differences are taken into consideration it is apparent that the pattern of usage of the 5 white-flowered trees was notably consistent. As the minimum distance between any two of these trees was approximately $\frac{1}{4}$ mile, there was probably very little overlap in the populations of most passerine species that were using them. Back and forth movements of lorikeets were much more likely, since they always travelled in flocks which appeared to range over wide areas. Consequently, usage data were least consistent for lorikeets, which at any moment were either present in numbers or altogether missing.

Lavender-flowered climbers.—The question of how as many as a dozen species of nectar-feeding birds can share a common food source may in part be answered by the degree of ecological isolation afforded by vertical stratification. The effectiveness of this behavioral mechanism in achieving a partial separation of potential competitors is indicated by the results from two flowering climbers. These enveloped the trunks of forest trees located at the edge of trails where more sunlight entered than in the heart of the forest.

Somewhat drooping horizontal branches carried at their ends large showy panicles of lavender campanulate flowers 4–6 mm across. The foliage and flowers were borne from about 15 feet above the ground to the base of the canopy at about 75 feet.

The combined results of 7 one-hour observation periods at two of these climbers located about 2 miles apart are given in Table 4. Of the 11 species of lorikeets and honeyeaters that were regular users of the white-flowered trees, seven were also frequent at the climbers. The four missing species were honeyeaters, *Toxorhamphus iliolophus* and the three *Myzomela* species, of which the *Myzomelas* had all shown strong affinities for the upper layer of the canopy. *Oedistoma pygmaeum*, which was also found to inhabit the upper canopy, was approximately 30 times less frequent in the climbers than in the white-flowered trees. The two honeyeaters that appeared in the climbers but not in the white-flowered trees, *Glycichaera fallax* and *Pycnopygius ixoides*, not unsurprisingly, are birds of the understory. *Glycichaera* is apparently a rarity at Karimui, since we were unable to obtain a specimen and have no other records of it.

On the basis of measured and observed vertical distributions of flower feeding birds at Karimui, we have compiled a list of species ranked in order of their presumed elevational preferences from the top of the canopy downwards (Table 3). By far the largest group (II) is composed of species that range more or less freely through a large part of the vegetational column. The *Myzomela* honeyeaters of group I appear to live exclusively in the high canopy from 80–150 feet above the forest floor. The birds of group III range up to 30–50 feet but rarely if ever use exposed crowns for feeding. Niche overlap between the species of groups I and III is thus almost entirely avoided. Maximum niche overlap occurs between the species within a group. Varying degrees of interaction can be expected between the birds of group II and those of groups I and III.

Overall usage of the flowering climbers, as with the white-flowered trees, was heavily dominated by lorikeets and honeyeaters (91 per cent). *Macropygia* sp. (6 per cent) and *Zosterops minor* (2 per cent) made up most of the remainder, the latter also having occurred less frequently in the white-flowered trees. The seven species that were regular in both the white-flowered trees and the climbers (*Trichoglossus haematodus*, *Charmosyna placentis*, *Oedistoma pygmaeum*, *Oreornis obscurus*, *Xanthotis chrysotis*, *X. polygramma*, and *Meliphaga* spp.) comprised 82 per cent of the total usage of the former and 83 per cent of the latter. This result implies particularly broad niche overlap between these species despite considerable differences between many of them in size and structure.

Hibiscus flowers.—A third type of flowering tree at Karimui deserves

TABLE 3

LIST OF BIRD SPECIES FEEDING ON FLOWERS IN THE KARIMUI REGION IN ORDER OF PRESUMED ELEVATIONAL PREFERENCE IN FOREST VEGETATION.

Variety of feeding trees used by each species is indicated in the right hand column.

F = flowers; SF = small fruits; *Ficus* = *Ficus* fruits; B = bark excrecence.

Group	Species	Elevational Preference	Classes of feeding Trees Visited
I	<i>Myzomela cruentata</i>	upper canopy only	F
	<i>Myzomela nigrita</i>		F
	<i>Myzomela eques</i>		F
II	<i>Oedistoma pygmaeum</i>	canopy and middle levels	F
	<i>Toxorhamphus iliolophus</i>		F
	<i>Charmosyna placentis</i>		F,B
	<i>Xanthotis polygramma</i>		F,SF, <i>Ficus</i>
	<i>Meliphaga</i> spp.		F,SF, <i>Ficus</i>
	<i>Xanthotis chrysotis</i>		F,SF, <i>Ficus</i>
	<i>Trichoglossus haematodus</i>		F, <i>Ficus</i> ,B
	<i>Oreornis obscurus</i>		F,SF, <i>Ficus</i>
III	<i>Zosterops minor</i>	middle and lower levels exclusive of canopy	F
	<i>Macropygia</i> sp.		F,SF
	<i>Pycnopygius ixoides</i>		F,SF

mention because of its location at the edge of a native garden perhaps a half-mile from the nearest forest. A small spreading tree of the *Hibiscus* tribe, it carried numbers of showy red blossoms 4 to 6 cm across. In one hour we recorded 2.4 bird-hours of usage, all by small bands of the sylviid, *Gerygone chloronota* (Table 4). These birds always moved together in groups of 2-6 and kept up a nearly continuous flow of soft vocalizations while they probed between petals at the bases of the large corollas. Although we visited this tree on several occasions, none of the forest nectar feeders was observed there. This negative result may not be significant in itself, but reinforces our general impression that open and second growth habitats in New Guinea have notably impoverished avifaunas in comparison, for example, with tropical South America (Diamond and Terborgh, 1967). The virtual absence of such habitats above 1,000 feet over most of the island prior to the recent expansion of the native population in the highlands is probably the explanation for this fact.

River Sena orange-flowered tree.—Observations at a fourth type of flowering tree were made at a locality lying a full day's walk to the northeast of Karimui at an elevation approximately 850 feet higher (about 4,500 feet). This tree overhung the north bank of the Sena River and was viewed con-

veniently from a large boulder in midstream. Its relatively small crown overtopped the nearby foliage and rose well over 100 feet above the forest floor. A heavy bloom of tiny flowers, 3–5 mm in diameter borne in dense heads, gave a yellow-orange cast to the whole crown. *Oedistoma* and *Myzomela* honeyeaters accounted for an unusually high portion of the usage (67 per cent), a finding that corroborates the observation that these species concentrate their feeding in the highest parts of the canopy. The species composition of the feeding assemblage was not one that would have occurred at Karimui. The presence of *Charmosyna pulchella*, *Myzomela cruentatus*, *M. rosenbergii*, and *Melidectes torquatus*, all absent or uncommon at Karimui, can best be attributed to the higher elevation of the Sena River site, since these are known to be montane rather than lowland forms (Mayr, 1941). The absence of some expected species (e.g., *Meliphaga* sp.) was perhaps due in part to the height and consequent exposure of this tree and to the fact that only one hour of observation was possible. Nevertheless, the total usage by families was in accord with the pattern that prevailed at Karimui, namely a predominance of honeyeaters (79 per cent), followed by lorikeets (20 per cent) and a very small remainder (1 per cent).

FEEDING ASSEMBLAGES IN FRUITING TREES

Most of the fruiting trees in which we found feeding birds could readily be placed in one of two categories: Those that bore small (< 5 mm) fleshy fruits and attracted a large variety of bird species, and those which bore larger (> 10 mm) fleshy fruits that were evidently unmanageable for small birds.

Small fruits.—We shall first consider trees with small fleshy fruits, in particular a set of three large strangling figs. These appeared, on examination of their fruits and foliage, to be of the same species, though possibly they were closely related species. All were of great stature (at least 100 feet), had broadly spreading crowns, and were heavily laden with soft pinkish fruits 4–6 mm in diameter. At Sordida (3,650 feet) one of these stood alone in an area that had been recently cleared for native gardens. The clearing was surrounded on all sides by forest which came to within 35 yards of the strangler. Another of these trees was located in dense forest at 3,500 feet in the bottom of a ravine about 14 miles southeast of Okapa Patrol Post. The third fruiting strangler was in montane forest at 5,800 feet near the Fore village of Miarassa.

The results of five, three and four observation periods at these three trees, respectively, are given in Table 4. The number of species that regularly fed in the stranglers was only slightly greater on the average than in the Karimui white-flowered trees, but included a notably greater variety of

families. Whereas each of the white-flowered trees at Karimui attracted eight to ten species of honeyeaters, none of the stranglers was used by more than three species of any family. Pigeons and honeyeaters were numerically dominant and accounted for 52–79 per cent of the total usage. Members of ten other families comprised the substantial remainder, again in contrast with the flowering trees in which the two principal families, honeyeaters and parrots, accounted for 91–99 per cent of the usage.

In consequence of the marked altitudinal turnover of bird faunas in New Guinea, the bird assemblages found in the three stranglers had very few species in common. The Sordida and Okassa trees shared only four out of a total of 25; the Sordida and Miarassa trees may have had one common species of *Meliphaga* out of 24, and the Okassa and Miarassa assemblages shared five out of 19. Members of four families occurred in all three of the stranglers and members of five more used two of them. In view of the great differences in habitat at each of the sites, such consistency implies that the pattern of usage of a given food source is to some measure independent of elevation and the particular species involved.

Some of the obvious differences in the data from the three stranglers can probably be ascribed to site-specific factors. The relative scarcity of honeyeaters in the Sordida tree and the abundance of *Mino dumontii*, a bird of second growth and edges, are surely due to its exposed position in a native garden. Low numbers of both species and individuals were recorded for the Miarassa tree, not as a result of low usage, but of exceptionally poor visibility of the crown from the only suitable viewing station.

Two additional species of trees with small (3–5 mm) fruits were the subjects of less intensive observations (Table 4). One was located in tall forest near Udo in the Karimui region and the other in old second growth near the Gimi Village of Mengino I on the west slope of Mt. Michael. The bird assemblages in these trees differed from those in the stranglers in attracting smaller numbers of species and families and in the preponderance of honeyeater usage. Since the results are based on only one and three hours of observation, respectively, the species lists are unrealistically low. Nevertheless, the scarcity (absence) of parrots, and the presence of pigeons, cuckoo-shrikes, whistlers, and flowerpeckers, is similar to the pattern found in the stranglers and quite unlike that of any of the flowering trees.

Large fruits.—Larger fruits were consumed almost exclusively by pigeons. Typical results are given in Table 4. The two trees held heavy crops of soft olive-sized fruits and in both the feeding was confined to two species of pigeons. In contrast with the sustained use of trees bearing flowers or small fruits, the presence of birds at sources of large fruits was sporadic and unpredictable. The trees were generally vacant for most of the day and when

a group of pigeons did arrive, it seldom remained for as long as an hour. Most of the flocks of feeding pigeons that came to the observer's attention contained a single species only. The large parrots and hornbills that might be expected to feed on large fruits in company with pigeons were never seen to do so. The population densities of these birds in the localities we visited were, however, low, and the large parrots are generally shy.

Ficus fruits.—An intriguing exception to the usual absence of passerine birds from trees with large fruits was uncovered in the case of three trees of a *Ficus* species (Table 4). Two were in tall forest along the Udo road near Karimui, while the third was in a grove of *Casuarina* second growth at an elevation of 5,800 feet near Mirassa. The fruits were ovoid-cylindrical, 6–8 cm in length and 3–4 cm in diameter. A thick woody pericarp precluded any direct assault on the sweet seedy pulp within. Nevertheless, examination of fallen fruits indicated that most had been entered by neatly cut holes, about 1 cm in diameter, in the blossom ends. Observation of the feeding birds soon disclosed that the holes were made by lorikeets. Tossing chips aside with a shake of the head, they gained access to the pulp within 5 minutes. Apparently, the side walls of the pericarp were invulnerable even to the lorikeets, because they always abandoned the fruits with most of the pulp remaining. The preopened fruits then attracted many other species, principally honeyeaters whose long and delicate bills are well-suited for probing but quite incapable of opening these fruits.

The second Udo *Ficus* (Table 4) was observed at an early stage in ripening when it held an abundance of unopened fruits which attracted lorikeets (> 99 per cent of usage), but before it contained sufficient numbers of opened fruits to be of interest to other birds. The first Udo tree and the Mirassa tree were at a later stage by which parrot usage had declined to only 8 per cent and 6 per cent, respectively, of the total. Honeyeater usage, on the other hand, had mounted to 90 per cent and 93 per cent.

A clear example of the dependence of feeding capabilities on bill structure, this extraordinary situation produced a pattern of tree usage reminiscent of both flowering and fruiting trees. The absence of pigeons and 95–100 per cent usage by parrots and honeyeaters are suggestive of the former, while the presence of cuckoo-shrikes, whistlers, and flowerpeckers is typical of the latter.

Bark feeding.—While at Karimui we encountered an active feeding tree whose attraction was apparently either a sap exudate or excrescences on the bark produced by an infestation. The several bands of parrots that were using this tree restricted their attentions to the smooth pale gray bark of the upper trunk and main branches (Table 4). All four species appeared to use the same method of feeding which consisted of slowly working up or down

TABLE 4 (Continued)

Hours of Observation	Flowers			Small Fruits			Large Fruits		Ficus Fruits		Bark Feeding			
	White-flowered trees	Lavender-flowered vines	River Sena flowering tree	Hibiscus flowers	Sordida strangler	Okassa strangler	Miarassa strangler	Mengino fruiting vine	Udo fruit tree	Okassa fruit tree		Sordida fruit tree	First Udo <i>Ficus</i>	Second Udo <i>Ficus</i>
<i>Cicinnurus regius</i>	18	7	1	1	5	3	4	3	1	1	1	3	1	3
<i>Paradisaea apoda rudolphi</i>	<1	<1	1	2	1									<1
Honeyeaters	53	79	78	4	4	66	10	88	88	88	88	90	1	93
<i>Glycichaera fallax</i>	8	3	32											
<i>Oedistoma pygmaeum</i>	3	<1												
<i>Myzomela eques cruentata</i>	1		17											
<i>nigrita</i>	10		1											
<i>rosenbergii</i>	<1		17											(t)
<i>Toxorhamphus iliolophus</i>	2													
<i>Melilestes megarhynchus</i>							3							<1
<i>Melipotés jumigatus</i>	<1		2											92
<i>Melidectes torquatus</i>	3	5												
<i>Oreornis obscurus</i>	8	19		3	37			7	10	(t)		3	24	1
<i>Xanthotis chrysolis polygramma</i>	6	11						2	2			17		

TABLE 4 (Continued)

Hoursof Observation	Flowers		Small Fruits				Large Fruits		Ficus Fruits		Bark Feeding				
	White-Flowered trees	Lavender-Flowered vines	River Sena flowering tree	Hibiscus flowers	Sordida strangler	Okassa strangler	Miarassa strangler	Mengino fruiting vine	Udo fruit tree	Okassa fruit tree		Sordida fruit tree	First Udo Ficus	Second Udo Ficus	Miarassa Ficus
<i>Meliphaga</i> spp. (\leq six species)	12	37	1	1	10	3	3	76	66	1	1	46	1	1	1
<i>Pycnopygius cinereus</i>					19	3	1	1	7						
<i>ixoides</i>		4													(t)
Unidentified honeyeaters	<1		10												
Flowerpeckers			1		4	14	3						<1		
<i>Dicaeum geelvinkianum</i>			1				2								
<i>Melanocharis longicauda</i>					4										
<i>versteri</i>															
<i>striativentris</i>															
White-eyes	<1	2													
<i>Zosterops minor</i>	<1	2													
Unidentified	1														
Total No. Species	17	16	7	1	15	14	10	9	9	2	2	7	2	7	4
Mean Total Bird-Hours	5.68	3.77	2.93	2.37	5.89	2.67	0.63	1.33	1.96	3.63	1.47	2.87	8.00	12.37	7.63

open sections of bark while chewing actively with the sides of their beaks pressed to the surface. Their efforts appeared to be concentrated around cracks, knotholes, and scars. The crown of the tree was nearly 100 feet above the viewing station and could not be seen in sufficient detail to permit identification of the food material.

The appearance of *Loriculus aurantiifrons* in this tree represents our only record of the species in the Karimui region. The other 3 parrots were common in the area and frequent visitors at feeding trees. *Charmosyna placentis* was the most abundant user of flowering trees but was not seen taking fruit. *Trichoglossus haematodus* regularly frequented both fruiting and flowering trees while *Psittaculirostris desmarestii* occurred commonly in fruit trees but was seldom attracted to flowers. Only in the present instance did we find all three species together in numbers that corresponded with our impression of their relative abundances in the local fauna.

NICHE OVERLAP IN FEEDING TREES

The number of bird species that use a feeding tree depends largely on the class of food available rather than on the particular species of tree (Table 4). Large fruits, bark excrescences, *Ficus* fruits, flowers, and small fruits, in that order, attract feeding assemblages of increasing diversity. High species totals for two of the flowering trees are the result of lumping data from more than one tree, whereas this was not done for any of the fruit trees. The fact that large fruits attract the least number of bird species and small fruits the most clearly illustrates the limitation that body size imposes on the size range of food taken. The high diversity of the assemblages that feed on small fruits results partly from the fact that the fauna contains a preponderance of small species and partly because the larger species often take small foods whereas the converse is not possible.

In trees bearing flowers, small fruits, or mature *Ficus* fruits we found only four instances in which more than 50 per cent of the bird usage was confined to the members of a single genus. The comparatively low niche overlap in three of these (Mengino fruiting liana, the *Hibiscus* and the *Miarassa Ficus*) was probably due to the location of the trees in second growth where the number of bird species is drastically lower than in the forest. The remaining case was the Udo fruit tree in which 66 per cent of the usage was by one to several species of *Meliphaga*. It is apparently rare that forest feeding trees are dominated to such an extent by one genus. Field identification of particular species of *Meliphaga* is at best difficult but at Karimui is rendered impossible by the presence of six species, five of which are scarcely distinguishable in the hand.

A quantitative estimate of the niche overlap in feeding trees can be obtained

TABLE 5

NICHE OVERLAP IN FEEDING TREES FROM THE POINT OF VIEW OF THE AVERAGE USERS.

The average user of a tree is the species whose usage brings the cumulative total to 50 per cent or more in a ranking of the species by usage.

Food Source	Average User	Per cent of Total Usage By Average User	Per cent of Total Usage By Species In Other Genera	Per cent of Total Usage By Species In Other Families
Flowers				
Karimui white-flowered trees (5)	<i>Myzomela nigrita</i>	10	86	47
Karimui lavender-flowered vines (2)	<i>Xanthotis chrysotis</i>	19	71	24
Sena River orange-flowered vines (2)	<i>Charmosyna pulchella</i> and <i>placentis</i>	<20	80	80
Small Fruits				
Sordida strangler	<i>Psittaculirostris desmarestii</i>	30	70	70
Okassa strangler	<i>Pycnopygius cinereus</i>	19	81	34
Miarassa strangler	<i>Pitohni dichrous</i>	10	90	85
Mengino fruiting vine	<i>Meliphaga</i> ssp.	?	24	12
Udo fruit tree	<i>Meliphaga</i> spp.	?	34	12
Mean			67	46

by computing the proportion of the total usage that accrues to the average user (Table 5). The average user is here defined as the species whose usage brings the cumulative total to 50 per cent or more in a ranking of the species by usage. In those cases in which the average user was identified to species it accounted for no more than 30 per cent of the total usage. Conversely, a mean of 67 per cent of the usage was by species in other genera and 46 per cent by species in other families in all the trees that contained either flowers or small fruits. It must be remembered that these figures are low estimates because of the probable but unrecorded utilization of these food sources by mammals, insects and even microorganisms.

DISCUSSION

In commenting on some feeding assemblages in Colombia Willis, (1966) concluded that because the food supply in most feeding trees appears to be superabundant, the competition between the species using them is probably insignificant. This inference tacitly depends on the regular availability of

feeding trees, an eventuality not borne out by our experience. We have on numerous occasions walked as much as an entire day in quest of feeding trees, both in New Guinea and in South America, without encountering a single one. The climate in the Eastern Highlands of New Guinea undergoes only a limited and irregular variation, yet it was our impression that flowering and fruiting of trees is highly sporadic. Similar impressions have been gained by botanists travelling in many parts of the tropics (Richards, 1952). Moreover, the high diversity of tree species in most tropical forests assures that individual feeding trees will on the whole be widely scattered. For example, Pries et al. (1953) found that the tree species of modal abundance in a *terra firme* forest in Brazil had a density of less than one individual per hectare. Thus the availability of suitable feeding trees to the bird species that habitually use them is by no means guaranteed.

The food supply in most feeding trees at the time of anthesis or ripening, as the case may be, is admittedly great. But as usage accumulates the amount of effort in searching that must be expended to procure a unit of nourishment will increase until the tree is no longer profitably exploitable. The period over which the remaining crop provides an adequate rate of feeding will depend on the intensity of usage. Exhaustion of the food supply in a feeding tree may often leave the local population without any equivalent alternatives. Thus when no feeding trees are available in the vicinity, many of the honey-eater species mentioned herein can be observed searching through foliage for insects, an occupation which yields food far less rapidly than the harvesting of feeding trees and which may not be sufficient when young are being fed. Even though food appears to be superabundant in most feeding trees, its current consumption can lead to scarcity at a later date when the supply has been exhausted. Hence the competition that at least potentially exists between the individuals and species that use a certain feeding tree must come as a result of the depletion of the standing crop and will be felt at a subsequent time, perhaps days or weeks after the tree received its heaviest use.

SPECIES-SPECIFIC BEHAVIORAL ATTRIBUTES AND THEIR RELEVANCE TO NICHE OVERLAP

The behavioral individuality of different species usually has the effect of lessening the niche overlap between them. Aggressive supplanting of one individual by another usually involved honeyeaters, most commonly, *Myzomela nigrita*, *Melidectes torquatus*, and *Xanthotis chrysotis*. The inherent aggressive tendencies of these species extended also to interspecific engagements. In the *Miarassa Ficus* quick aggressive responses of *Melidectes torquatus* towards *Melilestes megarhynchus*, *Pycnopygius cinereus* and *Melanocharis versteri* prevented individuals of these three species from using the tree for more than

a few moments at a time and seriously hampered their attempts to feed. In flowering trees at Karimui, *Xanthotis chrysotis* commonly displaced two other like-sized honeyeaters, *Xanthotis polygramma* and *Pycnopygius ixoides*, but reacted less frequently or not at all to the smaller *Meliphaga* spp. and *Oreornis obscurus*. In the Moluccas *Myzomela obscurus* supplants in flowering trees an equally small sunbird, *Nectarinia sericea* (Ripley, 1959). The apparent species-specificity of this type of behavior deserves further attention. The extent to which territoriality was involved in these interactions could not be ascertained, though very few collected individuals of these species were in breeding condition.

Specialized modes of feeding, even in trees that offer only one food source, can play a role in the competitive relations between species. The opening of *Ficus* fruits by parrots as a precondition for their further use by honeyeaters is a striking case in point. The possibilities in flowering trees are more numerous. Some species may concentrate on insects, others on nectar. In the white-flowered trees at Karimui we found that lorikeets (*Trichoglossus haematodus*) were actually feeding on the blossoms by biting off the receptacles and allowing the floral envelopes to fall to the ground. Destruction of flowers in a tree by one species palpably reduces its value to others that seek only nectar or insects.

Groups of birds using feeding trees cannot be considered flocks in the sense of socially integrated and temporally coherent units. For this reason we have chosen to use the word "assemblage" in connection with feeding trees, as discussed elsewhere (Diamond and Terborgh, 1967). Itinerant feeding flocks of the kind described extensively in the New World tropics by Davis (1946), Short (1961), Moynihan (1962), and in New Guinea by Archbold et al., (1942) do not exist at Karimui, though they occur in other parts of the island. Individuals and pairs of most species usually moved in and out of feeding trees independently of other members of the same species. Aside from the typically gregarious pigeons and parrots, movement in groups of more than two was noted only for *Gerygone chloronota*, *Mino dumontii*, *Oriolus szalayi*, *Gymnocorvus tristis*, *Diphyllodes magnificus*, *Paradisaea apoda*, *Oedistoma pygmaeum*, and *Zosterops minor*. With the exceptions of *Mino dumontii* and *Oedistoma pygmaeum* these species were infrequent users of feeding trees. The random movements of both species and individuals to and from feeding trees in New Guinea had the effect of maintaining in them nearly constant or only gradually changing levels of usage for periods of several hours.

The realization that supplies of tree-borne foods in the tropics are sporadic and local provides a rationalization of the wandering and gregarious habits of such birds as those parrots and pigeons that obtain their livelihoods almost

exclusively from tree products. Selection for the efficient utilization of widely scattered concentrations of food would favor capabilities for sustained high speed flight and rapid harvesting of the available food. Gregarious behavior permits an increase in the proportion of the harvest that accrues to the members of a species. Furthermore, it is only by associating in flocks that individuals can be led to trees that have been located previously by other members of their species. Particularly in the case of large carpophagous pigeons we noticed that the birds often flew great distances and then on arrival in a suitable tree would satisfy their appetites in a few minutes. In view of this tendency, underestimation of the niche overlap between gregarious species is likely when observations span only one or two hours of the day. Though large birds show a greater character divergence in bill length among sympatric congeneric species than do small birds, suggesting reduced overlap in the size range of food taken (Schoener, 1965), we cannot yet assess this prediction in the light of field observations.

BEHAVIORAL STEREOTYPY

A few years ago Klopfer and MacArthur (1960) and Klopfer (1962) advanced the notion that tropical birds are more stereotyped in their behavior than temperate birds and that the corresponding contraction of niches may underlie the high diversity of species in the tropics. In support of this idea it was assumed that older bird taxa (non-passerines) would show greater behavioral stereotypy than newer taxa (passerines), and then shown that the proportion of non-passerine species in local faunas tends to increase towards the tropics. However, it is not generally acknowledged that older taxa invariably possess inferior adaptive qualities or lack behavioral versatility (Mayr, 1963). Experimental tests of these hypotheses have recently led Klopfer (1967) to the conclusion that behavioral stereotypy is more likely to be an effect rather than a cause of tropical diversity.

An inspection of the list of species that regularly feed on flowers in the Karimui region (Table 3) suggests that New Guinea birds are highly variable in at least two measures of behavioral stereotypy: vertical range of foraging in the vegetation and food spectrum. Moreover, the correlation between stereotypy and phylogenetic status is low. That the composition of this list is not peculiar to Karimui is indicated by Ripley's (1964) observations of *Xanthotis chrysotis* and *X. polygramma* along with two species of *Myzomela* and three species of *Charmosyna* lorikeets in a flowering tree in western New Guinea. Group I is composed of species that were found only in the upper branches of tall trees. Moreover these three species, all in the genus *Myzomela*, appeared only in flowering trees. Thus the *Myzomelas* are specialists (show stereotypy) on at least two counts: their range of vertical move-

ment is restricted and their feeding appears to be limited to flowers. The three species that occurred only in the lower strata of the forest (Group III) showed somewhat more diversified feeding behavior. *Macropygia* sp. and *Pycnopygius ixoides* fed both on flowers and small fruits, though *Zosterops minor* was attracted only to flowers. By far the largest number of species (8) fell into Group II, those that ranged widely through the vegetational column. In this group are two species, *Oedistoma pygmaeum* and *Toxorhamphus iliolophus*, that apparently feed only on flowers while the remainder visit two or more classes of feeding trees. Thus in the Karimui fauna it is possible to recognize species that are specialists both in their vertical movements and in the variety of food taken, species that are specialists in either one of these but not in the other and species that are generalists in both.

The phylogenetic status of the specialist and generalist species is opposite to the predictions of Klopfer (1962) though the small sample is hardly adequate to show a general trend. The four species that are restricted both in their vertical movements and in food preference (the three *Myzomelas* and *Zosterops minor*) are all passerines. On the other hand two of the four non-passerine species (*Charmosyna placentis* and *Trichoglossus haematodus*) are diversified both in their feeding and movements and a third (*Macropygia* sp.) feeds both on flowers and small fruit though is vertically restricted in its foraging. These results reveal clearly the difficulty of generalizing about behavioral sterotypy in tropical birds.

NICHE OVERLAP

The very spotty attention that has been given to feeding trees in the Neotropics suggests that the diversity of competitors there is at least as great as in New Guinea, if not more so. Alvarez del Toro in Chiapas, Mexico (fide, Eisenmann, 1964) observed a flowering vine, *Combretum farinosum* (*Combretaceae*), which attracted 69 species of birds within a span of 20 days. How many of these were actually feeding is not mentioned. Similarly, in observations that extended over a 2-month period. Land (1963) accrued a list of 57 species that appeared in or around a fruiting tree (*Miconia trinervia*) in the Caribbean forest of Guatemala. At least 20 species, including members of 11 families, were seen taking fruit. In Panama Eisenmann (1961) watched 16 species of 7 families hawking termites around a nuptial swarm and compiled a list of 22 species of 11 families that he saw feeding on *Cecropia* catkins in the clearing on Barro Colorado Island. A high ratio of families to species was also found by us (Diamond and Terborgh, 1967) in the bird assemblages at two fruiting trees in the Amazonian forest of Peru. During observations of about 4 hours at each tree we recorded 11 species of 9 families in one and 16 species of 10 families in the other.

These results taken together suggest that high levels of niche overlap in feeding trees are the rule in the Neotropics as well as in New Guinea. Of course it can be argued that it is the spectacular and perhaps atypical occurrences that get into print. However, in the course of many days spent searching for feeding trees in New Guinea we found that the majority of flowering and fruiting trees did not attract birds of any kind. Apparently their products were unpalatable. All trees that did consistently contain birds are described in this paper. Since the results from the more active New Guinea trees are comparable to those reported from the Neotropics, we may conclude that diverse feeding assemblages are not at all exceptional phenomena, either in New Guinea or in the New World tropics.

At Karimui a group of five honeyeaters (*Meliphaga* spp., *Xanthotis chryso-tis*, *X. polygramma*, *Oreornis obscurus*, and *Pycnopygius ixoides*) occurred together in most fruiting and flowering trees, usually in the order of abundance listed from greatest to least. This order is in complete accord with our impression of their relative abundances in the overall fauna, which suggests that all these species are opportunistic and use feeding trees of almost any sort whenever they are available. Because it was rare to see at one time more than five individuals of any of these species, it can be surmised that a suitable tree draws individuals only from the immediate vicinity. Aside from the tendency to concentrate their feeding activities at slightly different levels in the vegetational column, the mutual niche overlap among them appears to be extensive. Whether spatial differentiation of niches, as discussed by MacArthur (1964) accounts for the coexistence of so many generalists is an important question that cannot be resolved without further study.

The pattern of usage of different food sources could serve as an objective basis for the identification of ecologically homologous components in altitudinally or geographically isolated faunas. For instance, in the montane forests around Okapa (5,800 feet) there occurs a group of honeyeaters, including *Meliphaga orientalis*, *Melidectes torquatus*, *Melipotes fumigatus*, and *Pycnopygius cinereus*, all of which feed both on fruits and flowers. Considerable mutual niche overlap among these species suggests that collectively they are the ecological counterparts of the five Karimui honeyeaters that were the subject of the preceding paragraph.

Combined data from 13 New Guinea feeding trees that contained either flowers or small fruits indicates that the species of mean abundance in the trees accounts for 30 per cent or less of the total usage. Usage by species in other genera (67 per cent) and other families (46 per cent) comprises a far greater proportion. A comparison of these results with similar data from a temperate locality could provide a useful test of the postulate that niche overlap tends to be greater in the tropics.

SUMMARY

A widespread phenomenon in tropical forest is the gathering of varied assemblages of birds in trees bearing fruits, flowers, or some other plentiful food source. Repeated censuses of such feeding trees lead to a time-dependent measure of feeding for each species present. Results from 20 feeding trees in the New Guinea Highlands indicate the breadth of the food spectrum of many species and the extent of niche overlap between different species.

Honeyeaters and lorikeets accounted for more than 90 per cent of the use of each of 3 different species of flowers. Small fruits attracted more diverse assemblages comprising many families among which honeyeaters and pigeons predominated. Larger fruits were taken almost exclusively by pigeons.

Evidence is presented that niche overlap in feeding trees is reduced to some degree by species-specific behavioral attributes. These include aggressive supplanting of individuals and specialized feeding techniques. Many regular feeding tree users displayed marked tendencies to concentrate their activities at particular levels in the vegetational column.

From the point of view of the average avian user of feeding trees, 67 per cent of the tree usage is by species in other genera and 46 per cent by species in other families, indicating broad niche overlap. The range of feeding behavior displayed by different species did not correlate closely with phylogenetic status and varied greatly from restricted to diversified.

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